SOME FEATURES IN THE ANATOMY OF THE SAPINDALES[1]

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(WITH PLATES II AND III)

In studying the phylogeny of plants, there are certain general principles upon which all conclusions are based. One of these deals with the retention of ancestral characteristics. A striking example of this is afforded by the anatomy of the cycads. The vegetative stem of these forms always has exclusively centrifugal metaxylem, but in the leaf petiole, the metaxylem is predominately centripetal, with only a slight development in a centrifugal direction. Centripetal wood structure is, of course, the more primitive, and its appearance in the leaf petiole of the Cycadales serves to relate them to their extinct Cycadofilicean ancestors, where centripetal wood was present in the stem. Similar bundles with centripetal wood are present also in the reproductive axes of certain Cycadales.[2]

Another well known seat of primitive conditions is the root, good examples of which are furnished by the Abietineae. The first and older subtribe, the Pineae, is characterized by the invariable presence of resin canals in the normal wood of both root and stem, while in the more modern subtribe, the Abietae, resin canals are generally absent in the normal wood of the stem. Resin canals do occur, in all four genera of the Abietae, in the center of the primary wood of the root.[3]

Recent investigations have shown that ancestral conditions may be recalled as a result of wounding. For example, these resin canals, present in the roots of the Abietae, are present invariably

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 42.

[2] SCOTT, D. H., The anatomical characters presented by the peduncle of Cycadaceae. Ann. Botany **11**:399–419. *pls. 20, 21.* 1897.

[3] JEFFREY, E. C., The comparative anatomy and phylogeny of the Coniferales. II. The Abietineae. Mem. Boston Soc. Nat. Hist. **6**:1–37. *pls. 1–7.* 1904.

in the wood formed immediately after injury. Anatomical evidence thus shows that there are present in the leaf, petiole, root, and wounded tissue of gymnosperms, structures quite unlike those normally occurring in the stem; and paleobotanical evidence shows that these are primitive features, retained in certain restricted localities long after they have disappeared elsewhere. Instance after instance could be cited where these two lines of evidence, anatomical and paleobotanical, reinforce each other in the gymnosperms. In the angiosperms, however, no such checking up is possible as yet, because of the comparative scantiness of fossil material. Here the anatomical principles worked out from a study of gymnosperms have to be relied on exclusively in tracing their phylogeny.

Another principle of comparative anatomy is that simple conditions are not necessarily to be interpreted as primitive. This is well recognized by zöologists, who regard tunicates as vertebrates which, in losing almost entirely their vertebrate characteristics, have reverted to a simpler ancestral organization, and as degenerate rather than primitive. Or, on the botanical side, *Abies* has as simple normal wood as any known; there are only two types of elements present, tracheids and parenchyma, transverse and longitudinal. In the roots of all species, however, there are specialized resin canals, surrounded by parenchymatous epithelial tissue; these are present also in the reproductive axes of certain species. Another complication is present in the wounded root of at least one species,[4] where above and below the parenchymatous ray cells there are rows of tracheidal cells, forming ray tracheids like those of *Pinus*. Applying the principles of comparative anatomy, it is evident that *Abies* is descended from forms which had both resin canals and ray tracheids, and its simplicity of wood structure is not primitive, but a result of degeneracy.

It is the purpose of this paper to present the conditions found in certain of the Sapindales, and then to interpret them in accordance with these principles. For this purpose, four representative genera were chosen; *Aesculus*, *Acer*, *Sapindus*, and *Staphylea*.

[4] THOMPSON, W. P. The origin of ray tracheids in the Coniferae. BOT. GAZ. 50:101–116. 1910.

Fig. 1 shows a transverse section of the wood of *Aesculus Hippocastanum* L., and fig. 2 a tangential section of the same. From these it is possible to make out the main features of the wood. Woods may be grouped into three classes, depending on the distribution of parenchyma: (1) a primitive type with only terminal parenchyma on the "face of the summer wood"; (2) a more advanced type with parenchyma scattered throughout the year's growth, that is "diffuse"; and (3) the highest type with parenchyma only around the vessels, or "vasicentric." *Aesculus* belongs to the third of these groups; furthermore, its parenchyma is chiefly on the tangential wall of the vessels. The mechanical elements of the wood also exhibit a high degree of specialization, in that they are all transformed to libriform fibers, with characteristically thick walls, and narrow, obliquely elongated simple pits. The vessels are scattered throughout the year's growth, giving the "diffuse porous effect." The vessels have pits on the side walls closely crowded together, but never fused, end walls with porous perforations, and tertially spiral thickenings on their inner walls. Thus in having vasicentric parenchyma, libriform fibers, and vessels with porous perforations, *Aesculus* has the wood structures characteristic of the highest dicots, but the rays present a peculiarly simple condition. They are always of the linear, uniseriate type, like those of many of the gymnosperms.

Figs. 1 and 2 represent *Aesculus Hippocastanum*, but the wood is practically indistinguishable from that of its near relative *Aesculus glabra* Willd., as well as other species of the genus, and this description applies equally to all.

Fig. 3 represents a tangential section of *Acer saccharum* Marsh. The wood is "diffuse porous" like that of *Aesculus*, and the parenchyma is likewise vasicentric, but less abundant, and instead of being on the tangential wall, it is on the radial wall. The libriform fibers are heavier than those of *Aesculus*, especially those immediately around the vessels, which are very thick walled, while those in the intervals are larger and thinner walled. The vessels are very similar to those of *Aesculus*, having porous perforations on the end walls, densely crowded pits on the side walls, and well marked tertiary thickenings. The rays, however, are strikingly

different. These are a few of the uniseriate variety, but the majority are multiseriate.

Figs. 4 and 5 represent transverse and tangential sections of the wood of *Sapindus* sp. Like the two genera described, the wood is "diffuse porous"; the parenchyma is vasicentric and abundant. The fibers are characterized by delicate cross partitions of cellulose, constituting the so-called "septate fibers." Though some of the vessels are small, the majority are large, serving at once to separate *Sapindus* from the other members of the Sapindales. They have porous perforations and spiral thickenings; the side walls in some places have closely crowded pits, but in other places there is a decided tendency toward fusing into rows of slitlike bordered pits. The rays of *Sapindus* are multiseriate, much like those of *Acer*.

Fig. 6 represents another member of the Sapindales, *Staphylea trifolia* L. Here the wood parenchyma is vasicentric, and usually on the radial side of the vessels. The wood elements are not as specialized as in the other genera; instead of being libriform or septate fibers, they are fiber tracheids, with thinner walls and conspicuously bordered pits. The vessels have both porous and scalariform perforations; the pits on the side walls are sometimes unfused like *Acer* and *Aesculus*, but are more often united to form large slit like openings. *Staphylea* is the only one of the four genera examined in which there are no spiral markings on the inner walls of the vessels. The rays range from 1 to 10 cells wide. These broad rays cause a local "dipping in" of the annual ring, like that in *Quercus*.

Having considered the general characteristics of these four members of the Sapindales, the question arises as to which is the most primitive and which the most advanced. Disregarding the evidence furnished by the ray, *Staphylea*, with its scalariform perforations and fiber tracheids, seem to be the lowest; but taking the ray structure into consideration, *Aesculus* seems to be the lowest. Thus the question narrows down to which is the more primitive for the Sapindales, uniseriate or multiseriate rays.

In this connection it is interesting to note the work of EAMES of this laboratory on the genus *Quercus*.[5] He found the rays of

[5] EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. **49**: 161–167. *pls. 8, 9.* 1910.

Quercus to be of two sorts, linear or uniseriate, and broad or compound. In investigating the relative primitiveness of these two types, he examined a fossil oak from the Miocene. Here he found the same two sorts of ray, uniseriate and broad, but the broad rays, instead of being homogeneous masses of parenchyma, were composed of smaller rays, separated from each other by fibers, or by fibers and wood parenchyma. This condition lead to the suspicion that broad rays of living oaks might be derived from the aggregation and fusion of small rays. Accordingly, he examined seedlings of a number of oaks, and found such to be the case. Seedlings of black oaks show, near the pith, a ray structure like that of the miocene oak, with a gradual, progressive fusion until a single, homogeneous, compound ray is formed. Seedlings of white oaks show a still more primitive condition. In some, for the first 15 or 20 years, only uniseriate rays appear, which generally fuse into compound rays. Thus both anatomical and paleobotanical evidence point to the conclusion that for *Quercus* uniseriate rays are primitive, and that the large rays are formed by a process of fusion.

This conclusion is further strengthened by a consideration of conditions found in wounded oaks. BAILEY[6] of this laboratory investigated a number of species of this genus, and found that in every case, after a severe wound, a broad ray breaks up into a number of uniseriate or small rays, a clear case of traumatic reversion.

This compounding process BAILEY has examined in a number of genera of the Betulaceae and Fagaceae, with similar results. For example, in *Alnus*[7] he finds all types, from exclusively uniseriate rays in *A. acuminata* H.B.K. to completely fused aggregate or compound rays in *A. rhombifolia* Nutt.

The uniseriate rays of *Aesculus*, therefore, are open to two interpretations; they may be primitive like those of white oak seedlings, in which case *Aesculus* has a very low type of wood structure; or they may be the result of reversion, in which case *Aesculus* is

[6] BAILEY, I. W., Reversionary characters of traumatic oak woods. BOT. GAZ. 50:374–380. *pls. 11, 12.* 1910.

[7] BAILEY, I. W., Relation of the leaf trace to the origin and development of compound rays in the dicotyledons. Ann. Botany (ined.).

descended from ancestors which had multiseriate rays like those of *Acer*, *Sapindus*, and *Staphylea*. In determining this point, one must rely on the principles of comparative anatomy worked out for the gymnosperms, and investigate the parts of a plant which are most tenacious of ancestral characteristics, namely, leaf petiole, reproductive axis, and root.

Figs. 7 and 8 represent transverse sections of the leaf petiole of *Aesculus Hippocastanum;* fig. 9 a tangential section of the same, and in all three the multiseriate type of ray is conspicuous. When a leaf petiole leaves the branch, there is no one woody cylinder, but instead, 20–30 small vascular strands. Most of these strands arrange themselves in the form of a circle, and fuse to form a siphonostele, but certain ones, perhaps 5–10, instead of taking up a peripheral position, remain in the center. These medullary bundles are at first collateral in structure, but soon the xylem begins to grow around the phloem, until they become amphivasal, forming bundles such as are found typically in monocot rhizomes. This siphonostelic condition with medullary bundles is found throughout the length of the petiole, up to the bases of the leaflets. Then the cylinder is broken again into a large number of vascular strands, which in the bases of the leaflets repeat the process carried on in the base of the petiole. Some take up a peripheral position and form a siphonostele, while one or two remain in the pith as medullary bundles. These medullary bundles, however, are always collateral, never amphivasal. The important point is that throughout the prevailing type of ray is multiseriate. This is equally true of the separate strands as they leave the main branch, of the woody tissue of the siphonostele of both petiole and leaflet, and of the medullary bundles of both petiole and leaflet. Usually the rays as they leave the pith are biseriate or triseriate; sometimes they remain so to the cambium, but usually they become reduced to a uniseriate condition. Another peculiar condition seen in tangential section is the longitudinal elongation of the ray cells.

It is one of the principles of plant anatomy that the leaf trace is tenacious of ancestral conditions, and it is interesting to note that in the case of *Aesculus* these primitive conditions are retained,

not only in the leaf trace, but also in the wood of the axis immediately around the leaf trace. Fig. 10 represents an outgoing foliar bundle; subtending it, there is a mass of ray parenchyma forming a true multiseriate ray. Often in the case of numerous small bundles going into the petiole, this mass of tissue extends all the way from one bundle to the next.

These photographs are all of *Aesculus Hippocastanum*, but the conditions of *Aesculus glabra* are essentially the same, except that under the leaf trace there is seldom as much parenchyma as here shown.

Fig. 11 is a tangential view of the wood of a root, showing an outgoing rootlet and the tissue immediately under it. The conditions are very much as in the branch, each rootlet trace being subtended by numerous multiseriate rays. Usually, however, this condition is not so pronounced in the root as in the branch.

Fig. 12 is a tangential section of a floral axis, showing the conditions immediately below an outgoing flower stalk or peduncle. The rays are characteristically biseriate, and extend sometimes a long distance below the trace. Often above the trace they are broader than below, but they never extend as far. The woody tissue is as a whole poorly developed, except at the end of each flower stalk, where it becomes much thicker. Just below the end, there are 5 or 6 traces going out simultaneously, each of which has a small number of multiseriate rays below it.

Three of the recognized primitive localities have thus been shown to have well marked multiseriate rays, and wounded wood was examined for the same structures. None were found, either because the injury was not sufficiently severe, or because the degeneracy of *Aesculus* has gone too far to be recalled traumatically.

Aesculus then presents a condition just the reverse of that found in *Quercus*. The former has uniseriate rays normally, with multiseriate rays persisting in primitive localities; the latter has compound rays normally, with uniseriate rays in primitive localities. Accordingly, multiseriate rays are primitive for the Sapindales, and *Aesculus*, instead of being the most primitive of the Sapindales, on the basis of ray structure, is really advanced, its simplicity being due to degeneracy.

Summary and conclusions

1. Investigations of the anatomy of living and fossil gymnosperms have proved certain general principles. One is that primitive structures occur in the fibrovascular bundles of the leaf petiole, the root, and the reproductive axis, and sometimes revert in wounded wood.

2. Of the Sapindales investigated, three show multiseriate rays normally: *Acer*, *Sapindus*, and *Staphylea;* the fourth, *Aesculus*, shows uniseriate rays normally, but multiseriate rays in the leaf petiole, root, and reproductive axis.

3. Applying the general principles enumerated above, it is evident that the multiseriate type of ray is primitive for the Sapindales, and that *Aesculus* is a degenerate member. Accordingly, the Sapindales belong high in any systematic arrangement of dicotyledonous woods.

In conclusion, I wish to express to Dr. E. C. JEFFREY my sincere thanks for his suggestions and advice during the course of this investigation.

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EXPLANATION OF PLATES II AND III

PLATE II

FIG. 1.—*Aesculus Hippocastanum;* transverse section of wood, showing uniseriate rays; ×80.

FIG. 2.—The same: tangential section of wood, showing similar rays; ×80.

FIG. 3.—*Acer saccharum:* tangential section of wood, showing multiseriate rays; ×80.

FIG. 4.—*Sapindus* sp.: transverse section of wood, showing multiseriate rays; ×80.

FIG. 5.—The same: tangential section of wood, showing similar rays; ×80.

FIG. 6.—*Staphylea trifolia:* tangential section of wood, showing multiseriate rays; ×80.

PLATE III

FIG. 7.—*Aesculus Hippocastanum:* transverse section of leaf petiole, showing multiseriate rays; ×180.

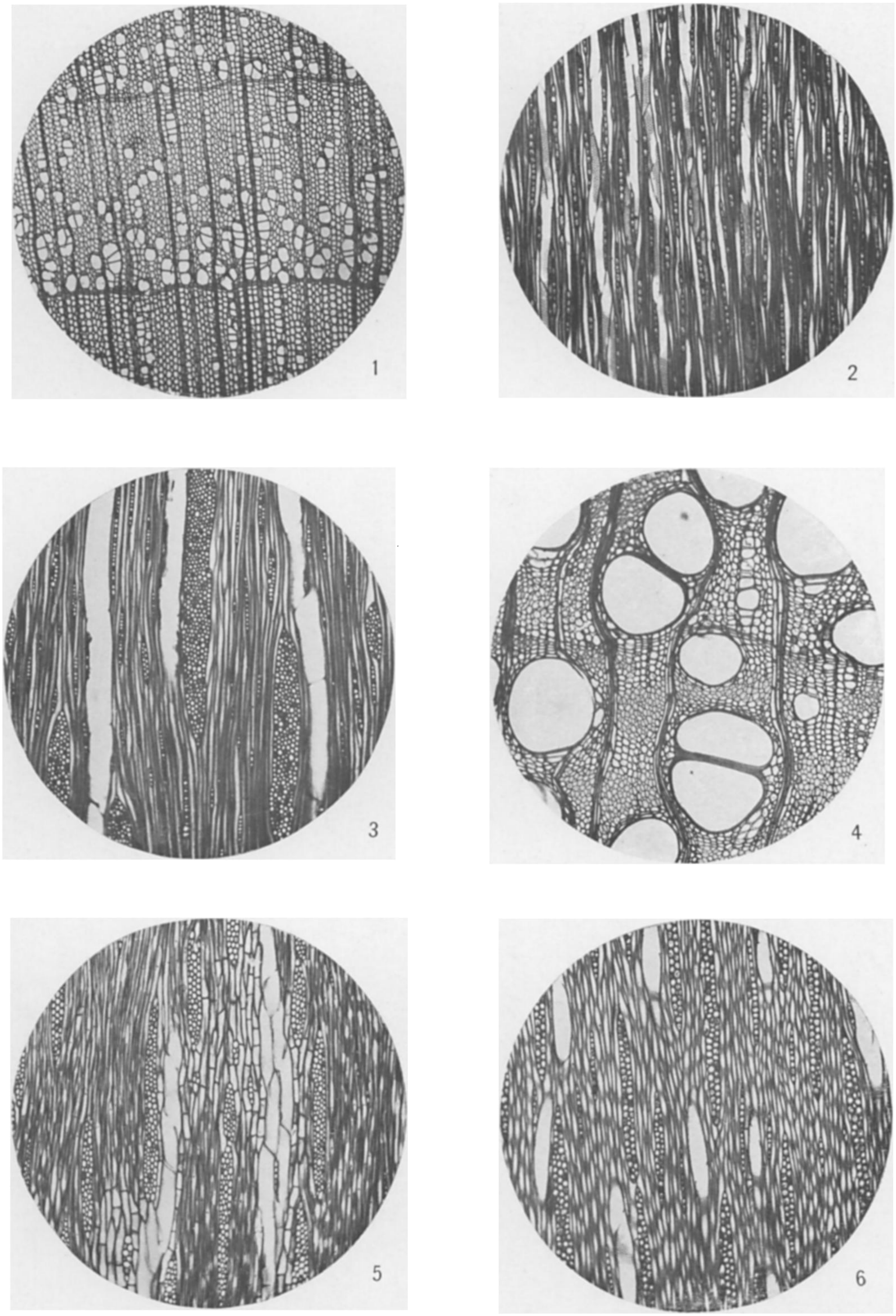
FIG. 8.—The same: transverse section of leaf petiole in another region, showing similar rays; $\times 180$.

FIG. 9.—The same: tangential section of leaf petiole, showing similar rays; $\times 80$.

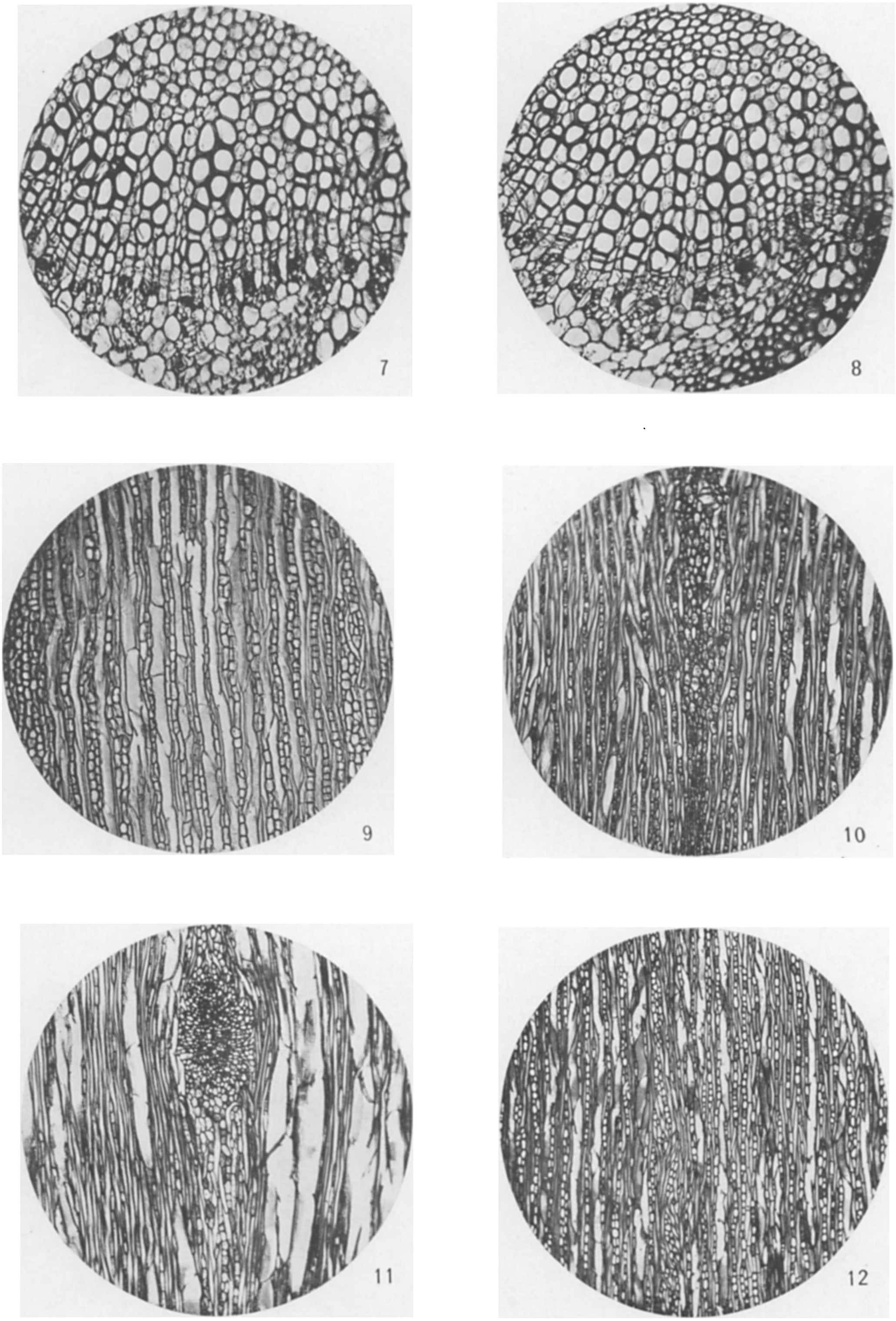
FIG. 10.—The same: tangential section of branch, showing outgoing foliar bundle with subtending multiseriate rays; $\times 80$.

FIG. 11.—The same: tangential section of root, showing outgoing rootlet with subtending multiseriate rays; $\times 80$.

FIG. 12.—The same: tangential section of reproductive axis, showing multiseriate rays below outgoing flower stalk; $\times 80$.



HOLDEN on SAPINDALES



HOLDEN on SAPINDALES